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Dear Editor,

I am pleased to submit a revision for "An Algorithm for the von Bertalanffy Seasonal Cessation in Growth Function of Pauly et al. (1992)" to be further considered as a Technical Note to *Fisheries Research*. The revisions in this manuscript are based on comments from two anonymous reviewers sent to me on 2-Sep-16 and on my rereading of the manuscript. Direct responses to both reviewers and a detailed list of changes to the manuscript are in the attached pages. I hope that you will find that the modifications to the manuscript both address the reviewers' concerns and have strengthened the document. Please feel free to contact me if you have any questions or concerns related to this submission.

Respectfully,

Dr. Derek H. Ogle
Professor of Mathematical Sciences and Natural Resources

Reviewer #1: Technical comments:

1. The methods section describes how starting values were selected manually or with the R function vbStarts. Were various starting values tried to ensure that nls achieved a globally optimal solution? This is recommended in the help file of vbStarts, but is more generally just good practice when using any optimizer.

DHO: I had not tried various starting values. However, I have now tried three other sets of starting values for each model fit and shown these results at the end of the Supplementary R code. Some alternative starting values led to a lack of convergence. In a few instances, alternative starting values led to different parameter estimates. However, in all of these instances, the overall fit (as measured by the RSS) was worse than for models with the reported parameter estimates. I did not report these results in the manuscript as I do not want to distract the reader from my main point (how to fit the Pauly et al. model). However, as mentioned above, this code is included in the Supplementary R code.

Also, relative to changes related to the reviewer's next comment, I no longer used the vbStarts() function to derive starting values. The methods were modified to describe this change.

2. I'd like to thank the author for providing the Supplementary R code. The code is easy to follow and well commented, and will be a useful reference for anyone attempting to apply the algorithm to other data sets. Unfortunately, when I ran the code, nls did not converge in two cases, showing the error message, "Convergence failure: false convergence (8)." (I'm using Rv3.3.0, which is the same version cited by the manuscript.) In the first case (Mosquitofish site 2, equation 3), I altered the starting values and was able to achieve convergence (same fixed ts and NGT starting values as for Bonito, and same site 2 results as shown in Table 1). Strangely, if I gave the solution (from Table 1) as starting values, it still failed to converge. In the second case (Mosquitofish site 4, equation 3), I was unable to find starting values that would result in successful convergence. I'm not sure where the problem lies, but this should be investigated, and perhaps the code could be made more robust before becoming publically available.

DHO: I can not fully confirm this, but I believe this issue may be related to the reviewer using a different operating system as a colleague noted the same problems using a Macintosh machine running 64-bit R. After further investigation, I believe that this problem largely stemmed from poor starting values. As such, I have used new starting values that were derived by visually fitting the VBGF rather than using the vbStarts() function. With these new starting values, I have not been able to recreate the convergence problems noted by this reviewer on my Windows machine, several other Windows machines, or my colleagues Mac machine.

3. I'm not aware of any theory that justifies using AIC when fitting by nonlinear least squares. It's typically used when fitting with maximum likelihood. That said, from a practical viewpoint, the application of AIC is internally consistent here, so I wouldn't expect model ranking to differ if maximum likelihood were used. However, it is possible that relative differences among models might change. I think this topic should be addressed in the manuscript, either by fitting with maximum likelihood, or by justifying the validity of AIC when using nonlinear least squares.

DHO: My methods follow the use of AIC for nonlinear models described in Ritz and Streibig (2008; p. 107), which I now cite in the revised manuscript. In addition, the likelihood values can be computed directly from the RSS values if, as done here, the residuals are assumed to be i.i.d. from a normal distribution (with a constant variance). With this, the AIC can be computed from the RSS (or with the least-squares method). This is from Burnham and Anderson (2002, p. 63).

4. In the Bonito example, it appears from Table 1 that the estimate of C in Equation 2 was at the upper bound of 1.0, in the original fit and in numerous bootstrap iterations. In some cases, such behavior can indicate that the optimizer got "stuck" at a local, rather than global, minimum. If that's an issue here, a logit transformation might help, such that the estimation is done in unbounded space, but is then transformed back into (0, 1) space. Or, the value of C might be fixed at C=1, in which case there would be one fewer estimated parameters, and consequently a lower AIC value. In this example, the lower AIC would likely result in a shift of which model was best.

DHO: In this situation, I followed the procedure used in Stewart et al. from where the Bonito data originated. I agree with the reviewer's comment (and I would not have constrained C), but I was attempting to show how, if the scientist is going to constrain C to be less than 1 as Stewart et al. did and the model results in C=1 that the Pauly et al. model may be a useful alternative. Thus, I have chosen to leave the model fitting process as in the original manuscript.

5. When looking at the data in Figure 3, I wondered whether they would be explained equally well (or better) by the common, non-seasonal von Bertalanffy model. And I think the answer is no. I fitted the common model for the Bonito data and Mosquitofish site 4 data, and the AIC values (based on nls for comparison) were higher than those of the seasonal models in both cases (Bonito AIC = 1444, Mosquitofish site 4 AIC = 4170). I didn't examine the other two data sets, but including this model alongside Equations 2 and 3 could strengthen support for the seasonal models. It might also be good practice for other studies, and therefore worth demonstrating in this paper, at the author's discretion.

DHO: It is not my intent with this manuscript to strengthen "support for seasonal models", rather it is simply to provide a method to compute the Pauly et al. model. However, I believe that the reviewer's comment that it is good practice to include the typical VBGF for comparison to seasonal models. Thus, I have added the typical VBGF to the results (which required modifying the format of Table 1), to Figure 1, and the R Supplementary Code. Furthermore, it should be noted that the bootstrapped confidence intervals in Table 1 were very slightly modified from the original manuscript because the random seed used to control the bootstrap results was modified by the addition of this new model.

Reviewer #1: Editorial comments:

44. This line could mention that the common von Bertalanffy function occurs as a special case when C=0 (i.e., equation 2 collapses to equation 1).

DHO: Done.

81-86. This section describes how the manuscript could fill a critical gap in the current state of knowledge. However, it's not really clear to me what exactly the prior deficiency is. I understand that t' is a function of estimated parameters. But, is this fundamentally different from many other nonlinear optimization problems where values are functions of estimated parameters?

DHO: I have attempted to modify this section to more clearly articulate the issue. The real problem is not so much that t' is a function of the estimated parameters (which I had stated in the original manuscript), but that t' must be derived from t, NGT, and ts and there is no mathematical equation that describes how to do this.

Unfortunately, in the absence of this equation, there also is no algorithm (prior to this manuscript) that describes (in any detail) how to derived t’ from t, NGT, and ts. So, the issue is really the complexity of the relationship between t and t’ and not the dependence of t’ on estimated parameters. Hopefully the new text better articulates this issue.

103-4. I was confused initially about what becomes a whole number, mostly because the example describes converting t=2.9 to 2.5, which isn't whole. I understood after reading step 2, but perhaps some more careful wording in step 1 would help avoid that confusion.

DHO: Generally removed reference to whole numbers as it is more clear to call this the “number of completed full growth periods.”

141. "I used …"

DHO: Fixed.

145. "divided by the quantity 1 minus …

DHO: This was removed because a different procedure was used to derive starting values.

156. Equation 3 fit slightly better, but the two models are really indistinguishable, given the common criterion that delta AIC < 2 for Equation 2.

DHO: Text was modified to address this correct concern. In addition, delta AIC values were added to Table 1 to better facilitate such comparisons.

Table 1. Mention in the table caption that the values in parentheses represent 95% confidence intervals, as stated in the Fig 3 caption.

DHO: Done.

Figure 2. I think the tick labels above and below the X-axis would be easier to read if the font size were a little smaller. I find the numbers somewhat difficult to distinguish.

DHO: Done.

Reviewer #2: remarks and suggestions:

Introduction

- Line 75. I agree that the way Beguer et al. (2011) fitted the function is not clear in the paper. Indeed, the equation was not really the one of Pauly as the authors dropped the implementation of t' because of the lack a comprehension of the original paper... . By the way, Linf was not fixed, but constrained so that it can not be upper than maximum L observed. The only difference with Pauly is that there is no loop-calculation of t'. Maybe a way to present it would be similar to the following one. This would also help to argue in favor of the present technical note to make this t' calculation clearer.

"...whereas, probably because of the lack of clarity of Pauly et al. (1992) on t', Beguer et al. used a modified version of Equation 3 without (the loop-calculation of) t', simply replaced by t in their equation."

DHO: I have re-read the Beguer et al. (2011) paper and it clearly states that they used the Pauly et al. (1992) model, even displaying the model in their Equations 2-4 (though, their interpretation of the parameters do not appear to be correct). In addition, on the second column of their page 607 it says "Contrary to fits within the classical VBG, the asymptotic length (Linf) of the seasonal VBG was fixed." There is no indication of how their t' was calculated (i.e., it did not suggest that my Equation 3 was modified replacing t' with t). In other words, none of what the reviewer says in this comment was evident from their paper.

I had contacted the first two authors (Beguer and Rochette) of the Beguer et al. (2011) paper when working on my manuscript. In that process, I reviewed their R script and did note that they did not actually fit the Pauly et al. (1992) model as their paper suggested. I considered using a personal communications in the current manuscript to note that Beguer et al. (2011) did not actually use the Pauly et al. (1992) model. However, in further communications with Rochette, who appeared to do the analysis for that paper, he noted that he had moved to another position and would not have time to pursue my questions of their work any further. To honor this, I did not pursue the personal communications angle and wrote the text that appears in the manuscript, which I believe to be accurate based on the published works of Beguer et al. (2011).

So, I am willing to make the changes that this reviewer has suggested, but I don't know how to cite it, as the information this reviewer suggests is not available in the Beguer et al. (2011) paper.

2.1. Calculating t'

- Line 95. ...the calculation of t' in equation 3 depends on...

DHO: Fixed.

- The six steps algorithm. The text of the six steps is well written but is difficult to keep in mind. As the author present this technical note in a way that equation 3 could be implemented in any nonlinear model fitting software, the text should help in presenting the equations of the loop calculation. Moreover, the examples chosen should be as much as possible refering to values chosen for Figure 2, which really helps the comprehension of the text. To not show to many equations, a balance could be found between clarifying the steps using representation (and values) of Figure 2, and using inline equations.

DHO: The steps of this algorithm do not ultimately result in a useful or simple equation. However, I take this comment as the reviewer wanting more clarity for the calculation of t'. I have attempted to provide more clarity by (a) providing example calculations for two ages underneath each step and (b) choosing ages and example parameter values that match Figure 2 (as suggested by this reviewer). From this, I also simplified (and, hopefully, clarified) some of the language in all steps and moved some of the information in Step 1 into the preceding paragraph.

2.2.
- Line 131. ... more appropriate fit than ... (not then, I guess)

DHO: Fixed.

- Line 138. This part of the sentence is grammatically strange to me : "Data from three locations were chosen to examine here to demonstrate..."

DHO: Modified.

3. Results … Line 156 - 160. Australian bonito data. Even if the AIC is lower, I would not say it is better with such a small difference. Parameter estimation are also quite similar and as the confidence intervals are provided, we can not really say that t0 are different. To me, the conclusion of this case is that there is no best model.

DHO: Similar comment to Reviewer #1 (for line 156). See response there.

4. Conclusion
- Conclusion is probably too fast. I agree saying that "equation 3 is likely not the globally best seasonal growth model", in particular with regards to the example of mosquitofish. In terms of purely statistical index using the AIC, Equation 2 is globally better. But, as mentionned in the results, Eq. 2 also respond "too dramatically" to part of the sample at site 2. Ecologically speaking, this drop should be questionned (but this is not the aim of the paper).
Equation 2 surely allows more flexibility in the fit of 'seasonnally varying' growth data. But, depending on species studied, the decline in size could be unreliable (in contrast to weight maybe). This requires a finer analysis of bounds of C, even fix C to 1.
I would say that Equation 3 is doing well for what it is supposed to do (as title suggests) : fit a growth with periods of "seasonal cessation in growth", which means size is not changing for a fixed period of time each year. However, using Equation 2 allows for more flexibility, thanks to parameter C that allows seasonal decrease, cessation or modified increase in size (or in weigth). When C=1, example of this paper showed similar results with Pauly equation. However, as shown by fit in Site 2, using a more flexible equation requires more caution in interpretation.

DHO: I am not sure that there are any modifications I need to make relative to this comment. I don't know what "Conclusion is probably too fast" means. The remained either fees like "discussion" that I hope to spur with this technical note or comments that are beyond the narrow scope and data of this short technical note. Thus, I have made not changes to the manuscript based on this comment.

Figure 2 … - As 'Winter Point (WP)' is not a parameter of the equation, it is called WP in a paragraph lost between the two equations. Could you remind the reader in the legend of this figure that WP is the Winter Point, to not search for it in the text. For the other parameters, we know where to look at them in the text as they are in the equation.

DHO: Done.

Documentation of Changes (line numbers from original manuscript)

31 – Removed “seasonal” … see comment for lines 90-91.

32 – Added comma after “Schnute and Fournier”.

36 – Added comma after “Bacon et al.”.

44 – In response to reviewer #1, changed “(C=0)” to “(i.e., reduces to Equation 1; C=0)”.

45 – Removed “for” from “(for 0<C<1)”.

50 – Changed “from” to “in”.

52 – Added period after “al” in “Huusko et al” and comma after “Huusko et al. (2011)”.

58 – Added comma after “Pauly et al.”.

60 – Changed “from” to “in”.

61 – Modified order of phrases. Now reads as “… devised Equation 3 from Equation 2 …”

83-86 – In response to reviewer #1, attempted to better explain why computing t’ is complicated. This resulted in a major modification to these sentences.

90-91 – Deleted “seasonal” and changed “Equation 2” to “Equations 1 and 2”. Thus, this statement is not focused on only seasonal growth models, but includes more general growth models. This changes follows the suggestion from reviewer #1 to include the typical VBGF.

95 – Added “in Equation 3” before “depends” in response to reviewer #2.

97-118 – Major modifications to the text describing the six steps and the paragraph leading into those steps. This is in response to reviewer #2. Section 2.1 now covers lines 97 to 130, whereas it covered lines 94 to 123 in the original manuscript. The editors/typesetters may have a better way to present the calculations (i.e., rather than bullets underneath the numerical headers), but these changes for clarification did not result in a substantially larger section.

121 – Added comma after “Team”.

122 – Added version number for FSA.

123 – Added comma after “Ogle”.

131 – Per reviewer #2, correctly changed “then” to “than”.

137 – Per reviewer #2, changed the first phrase of this sentence to read more easily.

141 – Per reviewer #1, changed this sentence so that it does not use “We used”.

142-146 – The description of the starting values was greatly modified as vbStarts() is no longer used. See my responses to reviewer #1 with regard to convergence issues in the R Supplement. Required adding the Ritz and Streibig (2008) citation.

148 – Added a sentence that multiple starting values were used to confirm finding the global minimum. Required adding the McCullough (2002) citation.

149 – In response to reviewer #1, noted that the AIC values was computed from the least-squares estimates because normally distributed errors with constant variances were assumed. In response to both reviewers, added a sentence that states that models with delta AIC values <2 are indistinguishable. These changes required adding the Burnham and Anderson (2002) citation.

152 – Added comma after “Baty et al.”.

156-160 – In response to both reviewers, rewrote these sentences to acknowledge that the fit of Equations 2 and 3 to these data were indistinguishable.

168 – Changed “i.e.,” to “e.g.”.

171 – Removed “carefully described” as that was pretentious.

173-174 – In response to both reviewers, modified this sentence to acknowledge that Equation 3 was not the “best” model in 3 of the 4 test cases.

175 – Removed “the” in front of “seasonal”.

Acknowledgments – Added reviewers and my colleague that helped me test the R Supplementary code on other operating systems.

References

- Added Burnham and Anderson (2002).
- Added Hota (1994) reference (it was cited but not included as a reference in the original manuscript).
- Added year and DOI for Huusko et al.
- Added McCullough (2008).
- Added DOI for Nickelson and Larson.
- Changed order of Ogle (2016a) and Ogle (2016b) because of other changes in the manuscript.
- Updated version number in R reference to v3.3.1.
- Added Ritz and Streibig (2008).

Table 1

- Had to completely reformat to include the results for the typical VBGF. Also added the delta AIC column.
- Values for confidence intervals were slightly changed due to inherent randomization in bootstrapping.
- Per reviewer #1, added note about 95% confidence intervals in caption.
- Modified caption to include the typical VBGF and delta AIC values.

Figures

- Slight modification of Figure 1 caption to make it clear that this was the Somers (1988) VBGF.
- Slight modification of Figure 2 caption to make it clear that this was the Pauly et al. (1992) VBGF. Also defined WP per reviewer #2.
- Added results for typical VBGF to Figure 3. Modified caption accordingly and made it clear which VBGFs corresponded to which Equation. Modified the font size on the axes as suggested by reviewer #1.

*Highlights (for review)

- The mathematical foundation of the seasonal cessation in growth model proposed by Pauly et al. (1992) is reviewed.
- An algorithm for implementing the seasonal cessation in growth model proposed by Pauly et al. (1992) in any software capable of performing nonlinear least-squares is proposed.
- Use of the algorithm is demonstrated with four sets of seasonal length-at-age data.

An Algorithm for the von Bertalanffy Seasonal Cessation in Growth Function of Pauly et al. (1992)

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Abstract

Pauly et al. (1992; Australian Journal of Marine and Freshwater Research 43:1151–1156) introduced a modified von Bertalanffy seasonal growth function that allowed for a period of no growth. Pauly et al. (1992) provided special purpose software to fit the model to length-at-age data but this software is no longer available and specific details to implement a critical aspect of the new growth function were not clear. I provide details for this critical aspect of the function, implement the function in the open-source R environment, and briefly demonstrate the use of this function with four data sets. With this, the growth function of Pauly et al. (1992) is now readily available to all scientists with access to software that can fit nonlinear models to data. Thus, this growth function may be implemented in more situations and its fit rigorously compared to the results from other models of fish growth.

Keywords: Growth, Seasonal, Cessation, Nonlinear Modeling

1. Introduction

The mean length-at-age for many fish (Haddon, 2011) and other aquatic animals (e.g., Hota, 1994; Harwood et al., 2014) is often modeled with the von Bertalanffy growth function (VBGF; von Bertalanffy, 1938). A common foundation for several parameterizations of the VBGF is

$$L_t = L_\infty(1 - e^{-q})$$

where L_t is the expected or mean length at time (or age) t, L_∞ is the asymptotic mean length, and q is at least a function of t. For example, the most common parameterization of the VBGF attributable to Beverton and Holt (1957) uses

$$q = K(t - t_0) \tag{1}$$

where K is a measure of the exponential rate at which L_t approaches L_∞ (Schnute and Fournier, 1980) and t_0 is the theoretical time or age at which L_t would be zero.

Many fish exhibit seasonal oscillations in growth as a response to seasonal changes in environmental factors such as temperature, light, and food supply (e.g., Bayley, 1988; Pauly et al., 1992; Bacon et al., 2005; Garcia-Berthou et al., 2012; Carmona-Catot et al., 2014). Various modifications of Equation 1 have been used to model these seasonal oscillations in growth. The most popular of these modifications, from Hoenig and Choudaray Hanumara (1982) and Somers (1988) with a clarification by Garcia-Berthou et al. (2012), uses

$$q = K(t - t_0) + S(t) - S(t_0) \tag{2}$$

with $S(t) = \frac{CK}{2\pi} sin(2\pi(t - t_s))$. In Equation 2, t_s is the amount of time between time 0 and the start of the convex portion of the first sinusoidal growth oscillation (i.e., the inflection point) and C is the proportional decrease in growth at the depth of the growth oscillation (i.e., "winter"). Equation 2 may represent no seasonal oscillation in mean length (i.e., reduces to Equation 1; C=0), a reduced but not stopped increase in mean length (0<C<1), a complete stop in the increase in mean length (C=1), or a decrease in mean length (C>1) during the “winter” (Figure 1). The point where the increase in mean length is smallest is called the "winter-point" (WP) and is at $t_s + \frac{1}{2}$ because the sine function in Equation 2 has a period (i.e., the growth period) of one year.

Pauly et al. (1992) argued that a decrease in mean length with increasing age is unlikely for organisms whose skeletons largely preclude shrinkage and, thus, values of C>1 in Equation 2 were unrealistic for length (but not weight) data (however, see Nickelson and Larson (1974), Huusko et al. (2011), and Garcia-Berthou et al. (2012)). Pauly et al. (1992) then proposed a modification to Equation 2 that included a no-growth period where mean length was not allowed to decrease. Specifically, their modification is

$$q = K'(t' - t_0) + V(t') - V(t_0) \tag{3}$$

with $V(\mathrm{t}) = \frac{K'(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(\mathrm{t} - t_s)\right)$. In Equation 3, NGT is the “no-growth time” or the length of the no growth period (as a fraction of a year) and t' is found by “subtracting from the real age (t) the total no-growth time occurring up to age t” (Pauly et al., 1992). Furthermore, because the units of K changed from $year^{-1}$ in Equation 2 to $(1 - NGT)^{-1}$ in Equation 3, Pauly et al. (1992) suggested using K' in Equation 3 to minimize confusion with K in Equation 2.

Pauly et al. (1992) devised Equation 3 from Equation 2 by assuming C=1 and replacing 2π with $\frac{2\pi}{1-NGT}$ (i.e., restricting the seasonal oscillation to the growth period and noting that K' only operates during the growth period). Their modification may be described geometrically (though not algorithmically) in two steps. First, Equation 2 with (fixed) C=1 is fit to the observed lengths and ages that have had the cumulative NGT subtracted (i.e., using t'). This growth trajectory is then separated at each WP and horizontal segments that are NGT units long are inserted at these points. This forms a growth trajectory over the real ages (t) that smoothly transitions into and out of the no-growth periods (Figure 2).

The growth function in Pauly et al. (1992) does not appear to have been widely used. Pauly et al. (1992) has been cited at least 70 times (from Google Scholar and ResearchGate searches on 31-May-16); though it appears that only two of 43 English journal citations (excludes book, dissertation, report, other non-journal citations, and journals not published in English) actually fit Equation 3 to data. Of these, Chatzinikolaou and Richardson (2008) used the special purpose LFDA software (www.mrag.co.uk/resources/lfda-version-50) to fit Equation 3 to length frequency data, whereas it is not clear how Beguer et al. (2011) fit the function, though they did fix L_∞ to a constant value.

Perhaps the growth function of Pauly et al. (1992) has not been widely adopted because it is not clear how to actually fit the function to length-at-age data. Pauly et al. (1992) provided a then ubiquitous but now obsolete 3.5-in "diskette" with a computer program to estimate the parameters of Equation 3; however, the last diskette has been lost and the source code is no longer available (D. Pauly, pers. comm.). Pauly et al. (1992) did describe the operations performed by their program, but there is no equation for t' or detailed description of how t' should be operationalized. This lack of specificity may limit use of Equation 3 because the relationship between t and t' is not a simple linear shift in scale, is not one-to-one, and depends on how t relates to t_s, NGT, and the number of completed no-growth periods prior to t.

Therefore, the objectives of this note are to (i) operationalize the calculation of t', (ii) provide an algorithm for the calculation of t' to be used when fitting Equation 3 to observed data, and (iii) illustrate the use of this algorithm with real data. With this description, Equation 3 can now be implemented in more situations and rigorously compared with other growth models (e.g., Equations 1 and 2).

2. Methods

2.1 Calculating t'

As noted by Pauly et al. (1992) the calculation of t' in Equation 3 depends on the observed age (t) and the cumulative no-growth time prior to t. In practice, the calculation of t' also depends on the position of the no-growth period within a year. Here, the position of the no-growth period is defined relative to the start of the no-growth period (SNG), which Chatzinikolaou and Richardson (2008) showed to be $SNG = WP - \frac{NGT}{2} = t_s + \frac{1}{2} - \frac{NGT}{2}$. With this, the following six-step algorithm may be used to compute ages adjusted for cumulative NGT prior to age t (i.e., t') from observed ages (i.e., t). Below each step are example calculations of t' for t = 1.4 and t = 3.0 assuming t_s = 0.05 and NGT = 0.3 which result in WP = 0.55 and SNG = 0.4 (as in Figure 2).

1. Subtract the SNG from t so that integer values are at the start of a growth period.
    - For t = 1.4: 1.4 - 0.4 = 1.0; and for t = 3.0: 3.0 - 0.4 = 2.6.
2. Subtract the number of completed full growth periods from the Step 1 result such that the remaining decimal represents the proportion completed of a year that started with the most recent growth period.
    - For t = 1.4: 1.0 - 1 = 0.0.; and for t = 3.0: 2.6 - 2 = 0.6.
3. Substract the NGT from the Step 2 result.
    - For t = 1.4: 0.0 - 0.3 = -0.3; and for t = 3.0: 0.6 - 0.3 = 0.3.

4. If the Step 3 result is negative, then the observed age is within the no-growth period and the negative value should be replaced with a zero. Otherwise, the positive value represents the amount of the most recent growth period completed.
    - For t = 1.4: -0.3 is replaced with 0; and for t = 3.0: 0.3 is not changed.
5. Add the Step 4 result to the product of the number of completed full growth periods (as used in Step 2) and the length of the growth periods ($1 - NGT$).
    - For t = 1.4: 0 + 1(1-0.3) = 0.7; and for t = 3.0: 0.3 + 2(1-0.3) = 1.7.
6. Compute t' by adding the SNG that was subtracted in Step 1 to the Step 5 result.
    - For t = 1.4: 0.7 + 0.4 = 1.1; and for t = 2.9: 1.7 + 0.4 = 2.1.

The t' values that result from this algorithm are then input values, along with observed lengths, to a function for fitting Equation 3 with any nonlinear model fitting software. For convenience, an R (R Development Core Team, 2016) function to represent Equation 3, including use of the algorithm to compute t', is included in the vbFuns() function of the FSA package v0.8.8 (Ogle, 2016a). Use of this function is demonstrated in the Supplementary information.

2.2 Demonstrating the Algorithm

The algorithm developed to fit Equation 3 is demonstrated with four data sets. The first data set is the fork lengths (mm) and decimal ages (the number of opaque zones observed on otolith thin sections plus the proportion of the year after the designated birthdate) from 215 Australian bonito (*Sarda australis*) sampled from commercial landings as detailed in Stewart et al. (2013). Stewart et al. (2013) fit Equation 2 to these data but constrained C to not exceed 1. These data were chosen to illustrate how Equation 3 may provide a better and more appropriate fit than Equation 2 with the boundary condition of $C = 1$. The remaining three data sets are for invasive Eastern mosquitofish (*Gambusia holbrooki*) from southern France to southern Spain detailed by Carmona-Catot et al. (2014). Standard lengths (mm) were measured for each fish and annual ages were estimated from length frequencies and analysis of scales, with decimal ages determined from capture date and estimated birth dates for a cohort. Carmona-Catot et al. (2014) fit Equation 2, without constraining C, to fish from ten locations. Data from three of these locations were chosen to demonstrate how Equation 3 fits relative to Equation 2 with varying estimates of C (i.e., C much greater than 1 for Site 2, C only slightly greater than 1 for Site 4, and C much less than 1 for Site 9).

The "port" algorithm in the nls() function in R was used to estimate the parameters for Equations 1, 2, and 3 for all four data sets. All starting values were obtained by visually fitting the VBGF to the observed data (Ritz and Streibig, 2008; Ogle, 2016b). Values of L_∞, K, and K' were constrained to be positive, t_s and NGT were constrained to be between 0 and 1, and C was constrained to be between 0 and 1 for the Australian bonito data and positive for the mosquitofish data. Alternative starting values were used to confirm that a global rather than a local minimum was obtained (McCullough, 2008). The growth function with the lowest Akaike Information Criterion (AIC) value, computed from least-squares results because normally distributed errors with a constant variance were assumed (Burnham and Anderson, 2002), was chosen as the better fit for each data set (Ritz and Streibig, 2008). However, if the difference in AIC between two models was less than 2, then the models were considered indistinguishable (Burnham and Anderson, 2002). Confidence intervals for each parameter were the 2.5% and 97.5% percentile values of non-parametric bootstrap parameter estimates computed with the nlsBoot() function from the nlstools package v1.0-2 (Baty et al., 2015) in R. All code used in these analyses is in the Supplementary information.

3. Results

The fit of Equations 2 and 3 to the Australian bonito data were indistinguishable (Table 1; Figure 3A). The t_s estimates were equal and the estimates of L_∞ and t_0 were similar between the two functions (Table 1). The length of the no-growth period was estimated with Equation 3 to be 0.13 or 13% of the year.

Equation 3 did not fit the mosquitofish data better in situations where there was some evidence for a decrease in mean length with increasing age (i.e., $C \gg 1$ in Equation 2; e.g., Site 2; Table 1; Figure 3B) or no evidence for a cessation in growth (i.e., $C < 1$ in Equation 2; e.g. Site 9; Table 1; Figure 3D). However, Equation 2 appeared to respond too dramatically to one sample of ages (approx. 0.4) at Site 2, and Equation 3 likely provides more realistic estimates of mean length throughout the seasonal cessation in growth period in this example (Figure 3B). Equation 3 fit better than Equation 2 when a cessation in growth was evident without an apparent decline in mean length with age for mosquitofish (e.g., Site 4; Table 1; Figure 3C).

4. Conclusion

The algorithm described here for computing t', which allows for Equation 3 to be statistically fit to seasonal age data, appears to provide reasonable parameter estimates for the four examples provided. Equation 3 is likely not the globally best seasonal growth model as demonstrated here with three of four data sets. However, perhaps a better understanding of the utility of the Pauly et al. (1992) growth function for modeling seasonal growth of fishes will be forthcoming now that this function is readily available to all scientists with access to software (e.g., R) that can fit nonlinear models to data.

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Supplementary Information

R code for all figures and analyses.

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Table 1. Parameter estimates (and 95% confidence intervals) from the fits of Equations (Eq) 1 (Typical VBGF), 2 (Somers (1988) VBGF), and 3 (Pauly et al. (1992) VBGF) to the Australian bonito and three sites of Eastern mosquitofish data. The Akaike Information Criterion (AIC) value and the difference in AIC from the minimum AIC for models fit to the same data (ΔAIC) are also shown for each equation.

	Parameter Estimates (95% Confidence Intervals)								
Eq	L_∞	K	K'	t_0	t_s	C	NGT	AIC	ΔAIC
				Australian Bonito					
1	77.32 (59.8,164.8)	0.22 (0.06,0.42)	--	-2.28 (-3.46,-1.48)	--	--	--	1444.3	8.9
2	71.9 (59.6,141.5)	0.27 (0.08,0.47)	--	-1.92 (-3.06,-1.13)	0.09 (0.00,0.20)	1.00[a] (0.44,1.00)	--	1435.9	0.05
3	71.7 (58.7,127.8)	--	0.31 (0.10,0.75)	-1.64 (-2.81,-0.70)	0.09 (0.01,0.16)	--	0.13 (0.00,0.46)	1435.4	--
				Mosquitofish (Site 2)					
1	66.8 (47.7,138.0)	0.28 (0.11,0.49)	--	-0.74 (-0.94,-0.59)	--	--	--	4355.8	196.4
2	35.9 (34.4,37.6)	2.01 (1.69,2.36)	--	-0.02 (-0.04,-0.01)	0.88 (0.87,0.89)	1.95 (1.84,2.05)	--	4159.4	--
3	35.1 (33.9,36.8)	--	4.64 (3.28,6.62)	0.43 (0.36,0.50)	0.92 (0.91,0.93)	--	0.43 (0.37,0.48)	4175.4	16.0
				Mosquitofish (Site 4)					
1	266.9 (70.7,623.6)	0.07 (0.03,0.35)	--	-0.72 (-0.79,-0.53)	--	--	--	4198.5	138.6

2	46.0 (40.3,56.7)	1.05 (0.64,1.55)	--	-0.20 (-0.28,-0.14)	0.75 (0.72,0.78)	1.28 (1.14,1.44)	--	4070.6	10.7
3	44.0 (39.0,58.0)	--	1.60 (0.88,2.55)	0.07 (-0.03,0.18)	0.76 (0.70,0.80)	--	0.26 (0.15,0.46)	4059.9	--
Mosquitofish (Site 9)									
1	46.7 (43.4,51.6)	0.86 (0.69,1.03)		-0.33 (-0.39,-0.28)	--	--	--	5031.5	35.7
2	41.6 (39.2,45.4)	1.31 (0.97,1.67)	--	-0.21 (-0.31,-0.15)	0.72 (0.65,0.77)	0.62 (0.45,0.78)	--	4995.8	--
3	47.0 (42.4,57.2)	--	0.77 (0.52,1.09)	-0.41 (-0.50,-0.18)	0.61 (0.55,0.65)	--	0.00 (0.00,0.27)	5018.4	22.6

[a]C was constrained to be less than or equal to 1 during model fitting.

Figure Labels

Figure 1. Example of Equation 2 (Somers (1988) VBGF) with L_∞=30, K=0.3, t_0=-0.1, t_s=0.05 (with WP=0.55) and four different values of C.

Figure 2. Example of Equation 3 (Pauly et al. (1992) VBGF) with L_∞=30, K'=0.35, t_0=-0.1, NGT=0.3, and t_s=0.05 (with WP=0.55). Each t_s is shown by a gray point, "winter point" (WP) by a vertical arrow, and no-growth period by the horizontal interval centered on the WP arrow and the gray region that extends to the x-axis. Ages adjusted for the NGT (i.e., t') are shown above the x-axis.

Figure 3. Fork lengths at age for Australian bonito (A) and standard lengths at age for Eastern mosquitofish at Sites 2 (B), 4 (C), and 9 (D) with the best fits of Equations 1 (Typical VBGF; dashed line), 2 (Somers (1988) VBGF; gray solid line), and 3 (Pauly et al. (1992) VBGF; black solid line) superimposed. Parameter estimates (and 95% confidence intervals) from the model fits are shown in Table 1.

Figure 1

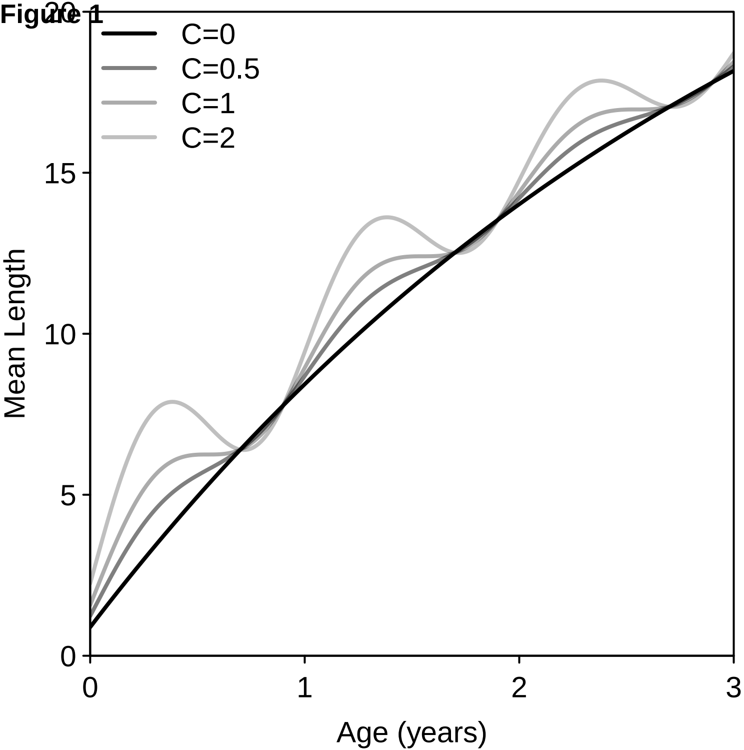
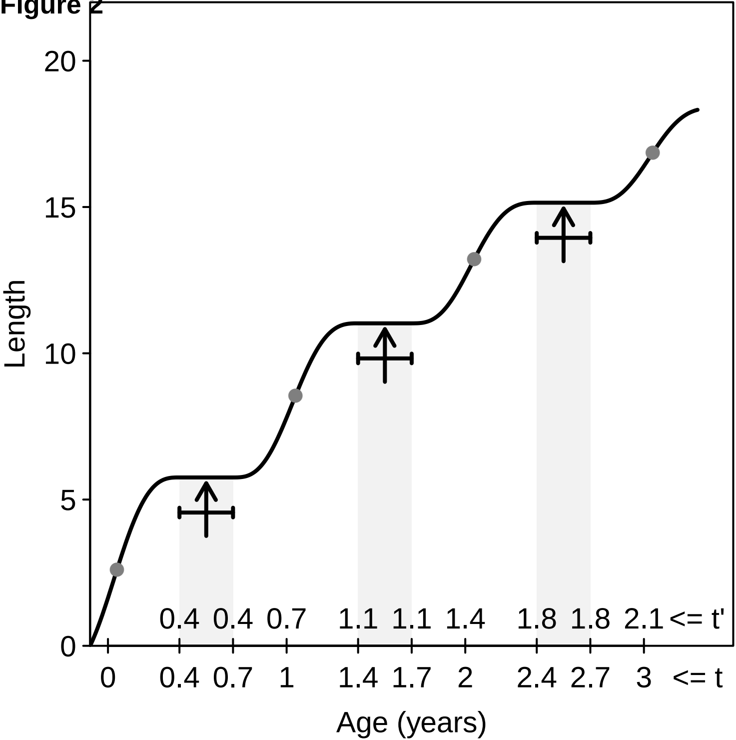
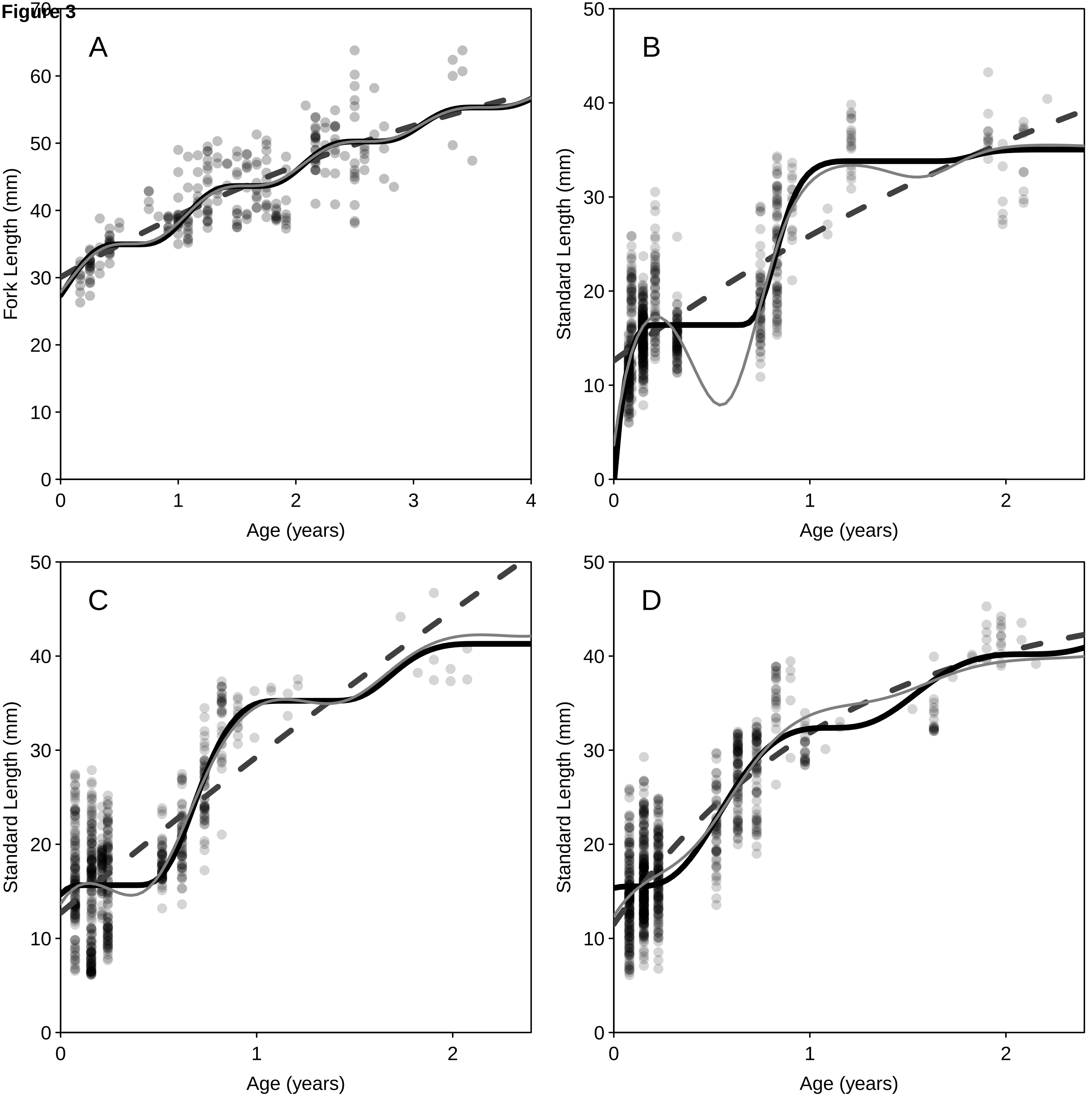


Figure 2



Length
20
15
10
5
0
0.4 0.4 0.7 1.1 1.1 1.4 1.8 1.8 2.1 <= t'
0 0.4 0.7 1 1.4 1.7 2 2.4 2.7 3 <= t
Age (years)

Figure 3


A
B
C
D
Fork Length (mm)
Standard Length (mm)
Age (years)
0
10
20
30
40
50
60
70
1
2
3
4

Supplementary material -- R Code
Click here to download Supplementary material for on-line publication only: SeasonalGrowth_Analysis.R